

# PROCEEDINGS OF THE UNITED STATES NATIONAL MUSEUM



SMITHSONIAN INSTITUTION  
U. S. NATIONAL MUSEUM

Vol. 108

Washington : 1958

No. 3391

## PYCNASPIS SPLENDENS, NEW GENUS, NEW SPECIES, A NEW OSTRACODERM FROM THE UPPER ORDOVICIAN OF NORTH AMERICA

By TOR ØRVIG<sup>1</sup>

### Introduction

In this paper a short description is given of a new ostracoderm, *Pycnaspis splendens*, new genus, new species, from the Upper Ordovician of the eastern slope of the Bighorn Mountains in north-central Wyoming. This new form is related to *Astraspis desiderata* from the Harding Sandstone, but it differs from the latter in the shape and microstructure of the tubercles of the exoskeleton. At the type locality it is associated with *Astraspis*? sp. indet. and *Eriptychiida* gen. and sp. indet. Exoskeletal plates referable to *Pycnaspis*, new genus, but at present indeterminable as to species are represented in the Winnipeg formation of the Williston Basin in Montana and in the Whitewood formation of the Black Hills in South Dakota, but such plates are missing entirely in the Harding Sandstone of Colorado.

Ordovician vertebrates from North America were first recorded by Walcott who, in 1892, described small exoskeletal plates of two forms, *Astraspis desiderata* Walcott and *Eriptychius americanus* Walcott, from the Harding Sandstone outcrops near Canyon City, Colo. These two forms Walcott referred tentatively to the Asterolepididae and Holoptychiidae, respectively, but they are now generally recognized as true representatives of the Heterostraci. Walcott also figured a third fossil from the Harding Sandstone, *Dictyorhabdus priscus* Wal-

<sup>1</sup> Curator, Department of Paleozoology, Swedish Museum of Natural History, Stockholm.

cott, which he regarded as the "calcified chordal sheath" of a fish allied to the bradyodonts, but which, as later researches have clearly shown (Dean, 1906, pp. 132-135; Bryant, 1936, p. 410; Flower, 1952, pp. 516-517), cannot possibly be of vertebrate origin. The Harding Sandstone vertebrate remains have been dealt with by Jaekel (in an appendix to Walcott's paper of 1892) and subsequently by, among others, Vaillant (1902), Eastman (1907, p. 33; 1917, pp. 236-239, pl. 12, figs. 5, 6), Woodward (1921, p. 179), Stensiö (1927, pp. 314-315, 333), Stetson (1931, p. 153), Bryant (1936), Berg (1940, pp. 107-108, 360-361), Kvam (1946, pp. 19-20, fig. 1), Gross (1950, p. 73; 1954, p. 80, pl. 3, fig. 2, pl. 5, figs. 3, 4, 7), Ørvig (1951, pp. 381-382, 387, 393, 415, 433, fig. 22 B, pl. 3, figs. 3, 4), Gregory (1951, vol. 1, pp. 102-104, vol. 2, figs. 6.2 (A), 6.3, 6.4), Denison (1956), J. D. Robertson (1957), and James (1957, p. 9, pl. 1). A description of *Astraspis desiderata*, based on the only fairly complete carapace of this form known so far,<sup>2</sup> will be given in a forthcoming paper by the present writer (Ørvig, in MS., b). Various notes on the invertebrate fauna and/or the stratigraphy of the Harding Sandstone have been given by Walcott (1892), Darton (1906b), S. R. Kirk (1929), Miller (1930), Stauffer (1930, p. 83), E. Kirk (1930), Branson and Mehl (1933); Behre and Johnson (1933), Ulrich (1938), Johnson (1944, pp. 320-322), Flower (1952), Frederickson and Pollack (1952), Twenhofel et al. (1954), Sweet (1954; 1955), and Denison (1956, pp. 368-369). This formation is now generally believed to be of Middle Ordovician (Trenton) age.

Vertebrates to some extent resembling those of the Harding Sandstone have long been known to occur in certain sandstone beds beneath the Bighorn Dolomite of north-central Wyoming and in the lower sandstone and siltstone members of the Whitewood formation of the Black Hills region in South Dakota, but none of this material has yet been properly described (see Darton, 1906a, p. 29; 1906b, pp. 550-551, fig. 3; 1909; Cockerell, 1913, p. 247; E. Kirk, 1930; Miller, 1930, p. 206; Romer and Grove, 1935, pp. 810-811; Furnish, Barragy, and Miller, 1936, pp. 1335-1338, pl. 2, figs. 14-16; Amsden and Miller, 1942, p. 304; Miller, Cullison, and Youngquist, 1947, p. 31; McCoy, 1952; Denison, 1956, p. 367). Dermal elements of Thelodontida and Osteostraci (*Ateleaspis*?) have been recorded from strata of a presumed lower Middle Ordovician age in the Bighorn Mountains of Wyoming (Tieje, 1924), but everything seems to indicate that those fossils are incorrectly determined. A new occurrence of Ordovician vertebrates has recently been detected farther north, in the sandstone and shale of the Winnipeg formation of the Williston Basin. This latter fauna,

<sup>2</sup> This specimen (USNM 8121), mentioned already by Walcott (1892, footnote on p. 167) and later described by Eastman (1917, pp. 238-239, pl. 12, figs. 5, 6) and by Bryant (1936, pp. 416-417, pl. 1), is of particular interest in that it shows part of the lateral line canal system on the anterior part of the carapace.

which is contained in drill cores from various places in eastern Montana, has proved to be of considerable interest, and together with other undescribed vertebrate material from the Ordovician of Wyoming and South Dakota it will be dealt with by the writer on a future occasion.

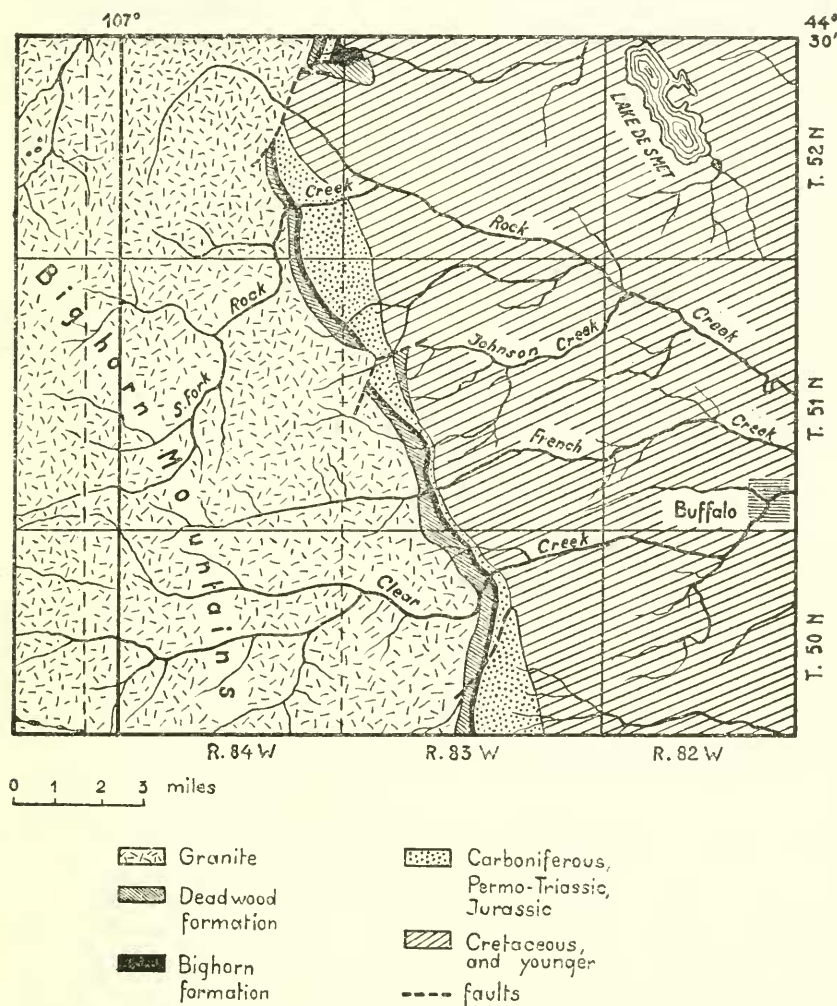


FIGURE 1.—Map showing the outcrops of Ordovician rocks on the eastern slope of the Bighorn Mountains in the area west of Lake De Smet and Buffalo, Johnson County, Wyo. Redrawn and to some extent simplified from the geological maps of the Bighorn Mountain Region published by Darton (1906a, pl. 47; 1906b, pl. 73).

The new astraspid, *Pycnaspis splendens*, new genus, new species, described in this paper comes from the Upper Ordovician deposits of the Bighorn Mountains of Wyoming. The histology of the exoskeleton in this form will be dealt with more in detail in another connection (Ørvig, in MS., a).

Fossils presumed to be remains of early vertebrates have been recorded on two occasions from North American deposits that are older than the Harding Sandstone of Colorado and the other vertebrate-bearing beds of Wyoming and South Dakota referred to above, viz.: (a) small, tuberculated plates from the Middle Cambrian St. Albans Shale of Vermont, described by Bryant (1927) and Howell (1937, pp. 1200-1202, p. 2, figs. 7, 8) under the name of *Eoichthys howelli* Bryant, and (b) *Archeognathus primus* Cullison, a peculiar V-shaped element with tooth-like cusps along one margin, which comes from the Lower Ordovician Dutchtown formation of Missouri (Cullison, 1938, p. 227, pl. 29, fig. 16a,b; Miller, Cullison, and Youngquist, 1947, pl. 1). It is by no means certain, however, if any of these fossils really are of vertebrate origin (Ørvig, 1951, footnote 1, on p. 381). The *Eoichthys* plates, at any rate, which I had the opportunity to study in 1953 during my visit to the department of geology of Princeton University, Princeton, N. J., cannot possibly have belonged to any true chordate. According to Rhodes and Wingard (1957, p. 453), *Archeognathus primus* is, in several ways, reminiscent of the Neurodontiformes (the "fibrous conodonts" of previous writers). Whatever its affinities are, this fossil cannot possibly be a detached cornu of an early representative of the Osteostraci (as tentatively suggested by G. M. Robertson, 1954, p. 733).

Outside North America, pre-Silurian vertebrates are only known with certainty from the lower Ordovician Glauconitic Sand of Esthonia. From these beds Rohon (1889) has described small tooth-like fossils belonging to two genera, *Palaeodus* and *Archodus*, which, by Russian paleoichthyologists, are nowadays referred to the Thelodontida (Obrutchev, 1948, p. 285; Bystrow, 1955, p. 473; Berg, 1955, p. 33; according to Denison, 1956, p. 367, they are indeterminable as to group). As will be shown in another connection (Ørvig, in MS., a), however, it is fully evident that *Palaeodus* represents broken-off tubercles from the exoskeleton of a form belonging to the Astraspida. That the Astraspida are met with not only in various places in the Cordilleran Region of the United States (Colorado, Wyoming, South Dakota, and Montana) but also in Northern Europe is a circumstance of some interest as it indicates that this ancient group of the Heterostraci may have had a worldwide distribution in Ordovician times.

METHODS AND MATERIALS: All of the specimens figured in this paper except two (figs. 1-3 of pl. 2 and figs. 1-4 of pl. 3) are contained in beds of Upper Ordovician age from the Rock Creek section on the eastern slope of the Bighorn Mountains. As far as can be judged from the limited material at my disposal, these beds are similar to the other vertebrate-bearing rocks from the Ordovician of North America in that they contain a thanatocoenotic assemblage of detached exo-



skeletal plates and scales, more or less fragmentary; however, no single specimen shows any of these elements in their natural association. The average size of the plates and scales is somewhat larger than that in the Harding Sandstone of Colorado and the sandstone and shale of the Winnipeg formation of the Williston Basin in Montana, and very small elements are missing altogether, a circumstance which probably indicates that the material has been sorted mechanically (by currents, etc.) prior to fossilization. The plates and scales have been abraded by rolling to some extent, but cannot, nevertheless, have been transported very far from their place of origin.

The state of preservation of the material is unusually favorable both for macroscopical and microscopical investigation. The plates and scales are easily freed of adhering sand-grains, e. g., by means of a sharp needle-scalpel, and the thin coat of reddish iron oxides which frequently obscures the fine details of their ornamentation can be removed, either with sodium hexametaphosphate or by boiling, for a very short time only, in a 10 percent solution of potassium hydroxide. The histological structure of the hard tissues is excellently displayed in those specimens which are light yellowish in color, but it has become obscured to some extent in those which are impregnated with iron oxides. For the preparation of exactly orientated thin sections, it is advantageous to embed the specimens in thin rods of acrylatic plastic by means of a bakelite press, according to the method recently described by the writer (Ørvig, 1957, p. 370).

The exoskeletal plates figured on plate 2, figures 1-3, and plate 3, figures 1-4, are from the gray, fissile shale of the Winnipeg formation of the Williston Basin (see, e. g., Ehlers, 1943, p. 1620; McCabe, 1954, p. 1998, fig. 10) contained in the drill core material from eastern Montana at my disposal. In this shale, which also exhibits phosphatic nodules, various invertebrate fossils such as lingulid shells, etc., and conodonts, the vertebrate remains are dark brownish or black. Their histological structure is frequently well preserved but is, in places, obscured by post-mortem changes caused by penetrative Algae or Fungi (see, e. g., Peyer, 1945; Bystrow, 1956).

It is worth mentioning here, finally, that the plates and scales of the Harding Sandstone—whose ornamentation is, in many cases, difficult to bring out satisfactorily by the ordinary methods of mechanical preparation—can be studied to great advantage on latex micro-moulds made from the impressions in the rock after the removal of the hard tissues with hydrochloric acid. A perfect reproduction of even very minute details of the ornamentation of those elements can be obtained by the method (described by Baird, 1955, p. 202; see also Gill, Caster, and Boswell, 1956, p. 198) of treating the etched surface of the sandstone with liquid detergent (e. g., Johnson

Wetting Agent 326) immediately before the first thin latex coat is applied.

All figured specimens belong to the U. S. National Museum. The technical work in connection with this paper has been carried out by members of the staff of the Swedish Museum of Natural History in Stockholm.

ACKNOWLEDGMENTS: For their generosity in placing Ordovician vertebrate material from a series of localities in North America at my disposal, I wish to express my indebtedness to Drs. P. E. Cloud, Jr. and R. J. Ross, Jr., of the U. S. Geological Survey in Washington, D. C., and Denver, Colo., respectively, and to Drs. A. K. Miller and W. M. Furnish of the University of Iowa. My thanks also are due to Dr. D. H. Dunkle of the U. S. National Museum for his kind assistance in procuring the material and to Dr. Jean M. Berdan of the U. S. Geological Survey, Washington, D. C., for her information concerning the stratigraphy at the type locality of *Pycnaspis splendens*, new genus, new species.

## Subclass PTERASPIDOMORPHI

### Superorder HETEROSTRACI

#### Order ASTRASPIDA <sup>3</sup>

##### *Pycnaspis*, new genus

DIAGNOSIS: A genus of the Astraspida of large size. Plates of the exoskeleton thick. Ornamentation in early stages of growth consisting of a shagreen of small tubercles exhibiting deep, radiating grooves on their crowns; in succeeding stages of growth consisting of stout, mushroom-like tubercles, smooth on top and ranging in outline from round to elongated or somewhat kidney-shaped. All tubercles consisting of an external layer of dentinous tissue and a basal portion of bone (aspidin) surrounding a "pulp" cavity. In tubercles belonging to early stages of growth the dentinous tissue is penetrated throughout its height by very fine canals originally housing cell-processes, and the aspidin is devoid of vascular canals issuing from the upper part of the "pulp" cavity. In tubercles of succeeding stages of growth the dentinous tissue in its basal part contains short, stemlike dentinal tubes which, in a superficial direction, rapidly subdivide into very fine ramifications, and the basal, bony portion is pierced by narrow, straight vascular canals radiating upwards and outwards from the roof of the "pulp" cavity and extending to about the boundary between the aspidin and the dentinous tissue.

<sup>3</sup> New rank, from Astraspidæ Eastman, 1917. Synonym: Astraspidiformes Berg, 1940.

TYPE SPECIES: *Pycnaspis splendens*, new species.

GEOLOGICAL OCCURRENCE: Upper Ordovician: Upper part of the Bighorn formation, eastern slope of the Bighorn Mountains, Wyoming. Middle Ordovician: Whitewood formation, "Icebox" shale, Black Hills Region of South Dakota; Winnipeg formation of Williston Basin, Montana.

REMARKS: The order Astraspida, comprising the genera *Palaeodus* Rohon, *Astraspis* Walcott, and *Pycnaspis*, new genus, has been defined in another connection (Ørvig, in MS., b). The diagnosis of *Pycnaspis* given here lists mainly such characters by which this genus is distinguishable from *Astraspis*.

The generic name is derived from the Greek *πυκνός*, thick, closely set, referring to the shape and distribution of the tubercles of the exoskeleton; and *ἀσπίς*, shield.

*Pycnaspis splendens*, new species

DIAGNOSIS: Same as for genus (single species).

HOLOTYPE: USNM 21333; detached exoskeletal plate, showing typical ornamentation (pl. 1, figs. 1, 2).

LOCALITY AND GEOLOGICAL HORIZON: The holotype and the other material of *Pycnaspis splendens*, new genus, new species, dealt with here were collected in 1951 by Dr. Jean M. Berdan, of the U. S. Geological Survey, at the South Fork of Rock Creek, center, N $\frac{1}{2}$ NE $\frac{1}{4}$ SW $\frac{1}{4}$ SW $\frac{1}{4}$ , sec. 25, T. 52 N., R. 84 W., Johnson County, Wyo. (locality number USGS 1362-CO; see fig. 1 and Darton, 1906a, p. 28). According to personal communication by Dr. Berdan, there follows, at this locality, on top of the massive Bighorn dolomite: (a) red shales ("Red Bighorn") containing a rich fauna of Upper Ordovician invertebrate fossils which seems to correlate with the Maquoketa of Iowa, including, e. g., *Lepidocyclus perlamellosus* (Whitfield), *L. cf. rectangularis* Wang, *Sceptropora facula* Ulrich, and *Streptelasma trilobatum* Whiteaves (cf. also the fauna list in Darton, 1906a, p. 28); (b) red and green mottled calcareous siltstones and sandstones; and (c) an upper sandy layer with numerous Ostracoderm remains. The latter is directly overlaid by the Lower Carboniferous (Mississippian) Madison formation. By weathering, the fossiliferous shales above the Bighorn Dolomite disintegrate into soil, and in this soil the vertebrate material was found. Since, however, the plates and scales always are associated with remnants of a coarse-grained sandstone, there is every reason to believe that they did not originally belong to the red shales but are, in fact, derived from the beds above, in all probability from the topmost sandy layer underneath the Madison Limestone or, in other words, from the very youngest part of the Bighorn formation exposed in the Rock Creek section.

There has been some difference of opinion in recent years concerning the correlation of the Bighorn formation with Ordovician strata elsewhere in the United States (see, e. g., Twenhofel et al., 1954). According to what has been said above, however, there can be little doubt with regard to the dating of the red fossiliferous shale which, in the Rock Creek section, follows on top of the massive dolomite members of this formation. Despite the fact that their exact position in the section cannot, at the moment, be made out with certainty, it is clear that the plates and scales of *Pycnaspis splendens*, new genus, new species, are no older than these red shales and that, therefore, they are of an Upper Ordovician age. It is true that there are also outcrops of red vertebrate-bearing sandstone beds underneath the Bighorn Dolomite in the Rock Creek section similar to those further south in the same area (see E. Kirk, 1930, p. 462; Amsden and Miller, 1942, fig. 1) but, according to Dr. Berdan (in litt.), there is no evidence at this locality of tectonic movements of such an order as to bring these sandstone beds in contact with the upper part of the Bighorn formation.

REMARKS: In the other material at my disposal, I have been able to identify some plates of *Pycnaspis* sp. indet., to some extent reminiscent of those of *Pycnaspis splendens*, new genus, new species, both in the sandstone and shale of the Winnipeg formation of the Williston Basin in Montana (pl. 2, figs. 1-3) and in a phosphatic conglomerate from the lower portion of the "Icebox" shale member of the White-wood formation of the Black Hills region in South Dakota (White-wood Creek section, near Deadwood). On the other hand, *Pycnaspis* plates and scales are missing altogether in all the numerous samples of the Harding Sandstone of Colorado which I have had the opportunity of examining in American and European museums, a circumstance which may be of some importance from the point of view of stratigraphy.

The specific name refers to the shining crown of the tubercles of the exoskeleton.

DESCRIPTION: In the material of *Pycnaspis splendens*, new genus, new species, one may distinguish thick exoskeletal plates and scales of mainly three different categories: (a) polygonal plates from the carapace; (b) ridge-scales, for the most part, at least, from the carapace; and (c) other scales probably belonging to the trunk behind the carapace. The polygonal plates and ridge-scales are in several respects rather reminiscent of those in the carapace of *Astraspis desiderata* (Ørvig, in MS., b), and everything goes to prove that they originally occupied much the same position in relation to each other as in the latter form. Thus, the ridge-scales very likely are detached components of a system of longitudinal crests extending, like in *Astras-*



*pis*, over the whole post-orbitopineal portion of the carapace (Eastman, 1917, p. 239, pl. 12, figs. 5, 6; Bryant, 1936, pp. 416–417, pl. 1; Ørvig, in MS., b), and possibly continuing backwards on to the trunk behind the carapace, and the polygonal plates probably formed a fairly regular pattern in the interspaces between the crests and anteriorly to

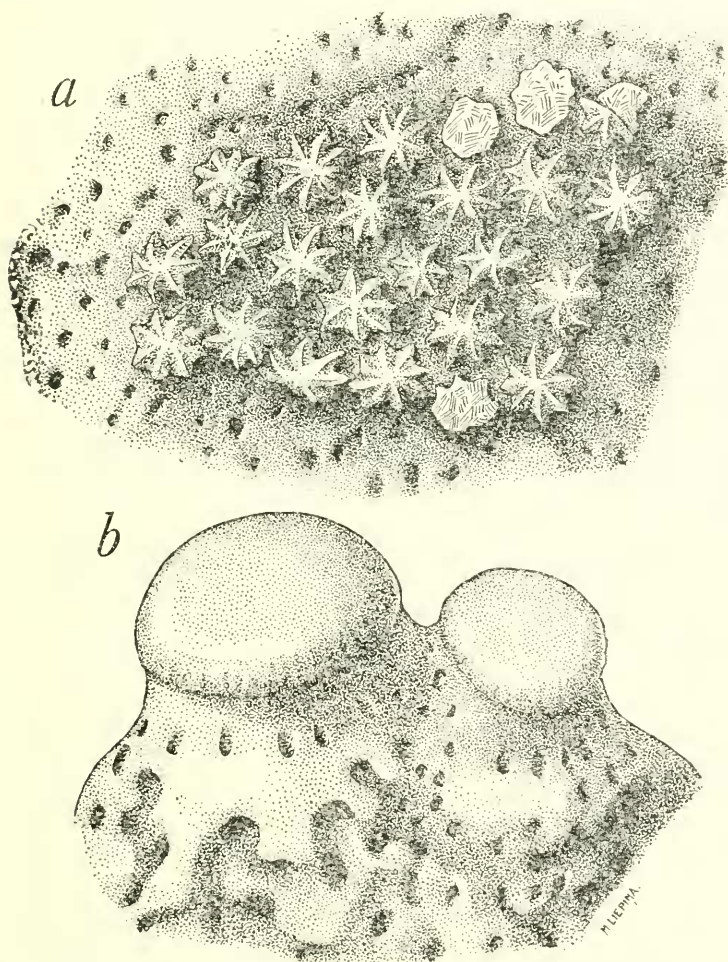


FIGURE 2.—*Pycnaspis splendens*, new genus, new species. Ornamentation of the exoskeleton: *a*, shagreen of small tubercles belonging to an early stage of growth, in superficial view (mainly after USNM 21334,  $\times 30$ ); *b*, large tubercles belonging to a late stage of growth, in oblique lateral view (USNM 21335,  $\times 30$ ).

them. On the other hand, there are no plates and scales in the material similar to those which, in *Astraspis*, exhibit shallow lateral line grooves on their external face (Ørvig, in MS., b; see also Walcott, 1892, pl. 4, fig. 1). If not purely coincidental, this circumstance may

either mean that the lateral line system was rather incompletely developed as compared with that in *Astraspis*, or, perhaps still more probable, that it was situated to a large extent in canals in the interior of the exoskeletal elements so that it was invisible in external view (cf. in the Eriptychiida, p. 18).

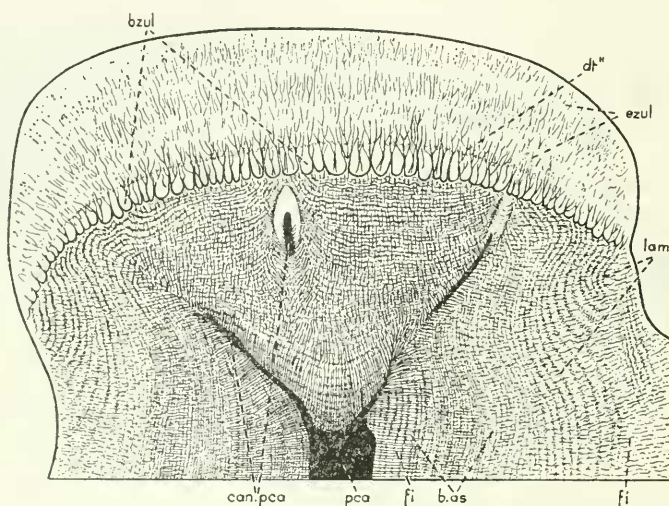


FIGURE 3.—*Pycnaspis splendens*, new genus, new species. Vertical section of a tubercle of the exoskeleton (section No. S 1477, from Ørvig, in MS., a;  $\times 150$ ). Explanation of symbols: *b.as*, aspidin; *bzul*, inner part of dentinous tissue; *can. pca*, vascular canals issuing from the upper part of the "pulp" cavity; *dt'*, fine ramifications of dentinal tubes; *ezul*, outer part of dentinous tissue; *fi*, fibers of Sharpey; *lam*, concentric lamellation of aspidin; *pca*, "pulp" cavity.

The polygonal plates of the carapace, which are most commonly met with in the material, are generally elongated rhomboid or more or less distinctly pentagonal in shape. They are often somewhat convex externally, but as far as I can find they are not raised upwards into a central cone-like prominence as frequently is the case in *Astraspis*. In some places they overlap each other to some extent, but as a rule they show no imbricating arrangement, being situated beside each other in much the same manner as the exoskeletal units, e. g., in the carapace of *Tesseraspis* (Wills, 1935), in the cephalic shield of certain late Osteostraci (Ørvig, in MS., a), and in the armor of various Ostraciontidae.

The ridge-scales, which are symmetrical, vary to some extent where their shape is concerned. Thus, some of them—which, judging by the condition in *Astraspis desiderata* (Ørvig, in MS., b), quite conceivably occupied a position in the anterior half, or thereabouts, of the longitudinal crests of the carapace—are longer than broad and

have a truncated, or slightly rounded, posterior margin (pl. 1, figs. 3-6). Others, which probably were situated further backwards in the crests, are equally as long as broad, and their posterior margin is more or less obtusely V-shaped. In all the ridge-scales one may, just as in those of *Astraspis desiderata*, distinguish the following faces: (a) a convex external face, consisting of an anterior portion which slopes forwards and downwards and which is overlapped by the ridge-scale in front (*od<sub>a</sub>*, pl. 1, figs. 3, 4), and a posterior, exposed portion ornamented with tubercles throughout its extent (pl. 1, figs. 3, 4); (b) a concave basal face having the appearance of a broad, longitudinal groove (*bf*, pl. 1, figs. 5, 6); (c) a concave posterior face overlapping the anterior portion of the external face of the ridge-scale following next behind (*og<sub>p</sub>*, pl. 1, figs. 5, 6); and, finally, (d) a paired lateral face, a little concave and sometimes fairly low, overlapping the adjoining polygonal plates on each side (*og<sub>l</sub>*, pl. 1, figs. 3, 5). As fully evidenced by their structure, the ridge-scales were firmly attached to each other. In the material at my disposal, however, there is no indication whatsoever that they tended to fuse with their fellows in the individual crests in the same manner as in *Astraspis desiderata* (Ørvig, in MS., b).

The scales presumably belonging to the trunk behind the carapace are far less common in the material than the polygonal plates of the carapace and the ridge-scales. They are more or less rhomboid in shape, frequently broader than long, and deeply imbricating. Their external face is made up of a large anterior overlapped portion and a fairly narrow posterior exposed portion ornamented with tubercles. Scales of this particular kind are, as far as I can find, not met with in the *Astraspis* material from the Harding Sandstone or from other formations.

The ornamentation of the plates and scales is subject to considerable variation. Some of the elements that are clearly preserved in early stages of growth show an immature type of ornamentation, made up of a shagreen of fairly small and low tubercles (fig. 2, *a*, cf. *t<sub>a</sub>*, pl. 1, figs. 1, 2, 4), which in superficial view are rather similar to those on the exoskeleton of various Psammosteida and certain Osteostraci as well (see Obrutchev, 1956, pl. 1, fig. 4). These tubercles are highly reminiscent of those in *Astraspis* (fig. 4; Walcott, 1892, pl. 3, figs. 13, 14; Bryant, 1936, p. 418, pl. 2, fig. 2), and are, in fact, only distinguishable from the latter by the circumstance that, in the individual plates and scales, they are remarkably uniform in size and, as a rule, placed close beside each other with about equal interspaces. They consist of a bulbous crown, exhibiting deep grooves radiating in a basal direction from the apex, and a fairly low neck-portion which is somewhat constricted below the crown but otherwise not sharply defined from the latter.



In the great majority of the plates and scales, on the other hand, the early shagreen of starlike tubercles has, during subsequent stages of growth, been supplanted completely by another, mature type of ornamentation consisting only of thick, mushroom-like tubercles (fig. 2, *b*; *t*<sub>6</sub>, pl. 1, figs. 1, 2, 4), frequently of large size, which are in several respects different from those on the exoskeleton of *Astraspis*. In top view the crown of these tubercles is rounded, elongated, or even somewhat kidney-shaped; it is always smooth and shining superficially, and at its basal circumference it is generally more or less crenulated. The neck-portion of the tubercles, which is always well developed, is a little constricted immediately below the crown, and is separated from the latter by a distinct nick. Contrary to what might be expected in view of the state of preservation of the material, the smoothness of the crown is certainly a primary condition. As in *Astraspis* (Bryant, 1936, p. 418, pl. 2, fig. 1), the tubercles were in certain cases subject to some post-mortem abrasion, but, as far as I can find, this cannot possibly account for the fact that in tubercles of different height, situated close together, and sometimes even partly superimposed on each other, the crown invariably shows the same smoothly rounded contour in vertical section.

In the material of *Pycnaspis splendens*, new genus, new species, at my disposal, at a rough estimate only 0.4 percent of the specimens (6 out of a total 1,500, or more) display both the immature and mature types of ornamentation simultaneously (e. g., the holotype, pl. 1, figs. 1, 2). If such specimens were lacking altogether—which might easily have happened in a less comprehensive material—one should no doubt refer the plates and scales, where the ornamentation is of the immature type (fig. 2, *a*), to another species and (in view of the microstructure of the tubercles, see below) probably even to another genus than those where it is of the mature kind only (fig. 2, *b*). It is true that, as far as one can tell, a correspondingly marked and abrupt change in the ornamentation of the exoskeleton with advancing age is not met with in any other representative of the Heterostraci and rarely, if ever, in placoderms and early teleostomians either (cf., e. g., in *Bothriolepis*, Stensiö, 1948, pp. 169–171, 376–386). But the condition of *Pycnaspis splendens*, new genus, new species, referred to above nevertheless shows that in dealing with early Paleozoic bone bed material from the taxonomic point of view one has, at least in certain cases, to allow for a considerable margin of error.

It is worthy of mention, finally, that the ornamentation of the plates and scales was subject to variation not only in different stages of growth but even to some extent in different parts of the body. Thus in the polygonal plates, which presumably lay mainly on the anterior portion of the carapace, all tubercles, large and small alike, rise straight



upwards and are blunt on top (fig. 2, *b*, pl. 1, fig. 2). On the other hand, in the ridge-scales of the longitudinal crests and in the polygonal plates which probably occupied a position in the interspaces between these crests on the posterior portion of the carapace, the tubercles are inclined backwards (pl. 1, figs. 3, 4) and are frequently tapering

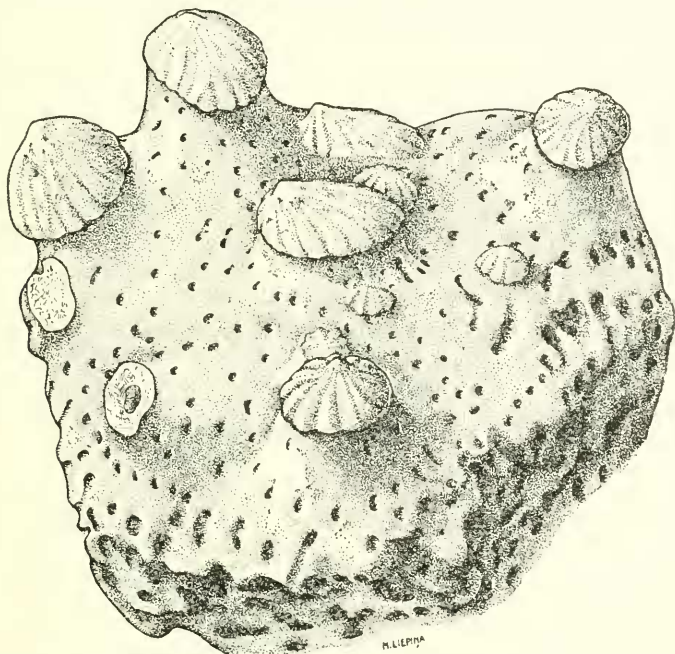


FIGURE 4.—*Astraspis?* sp. Large exoskeletal plate from the *Pycnaspis*-bearing beds of the Rock Creek section, in oblique lateral view. (USNM 21338;  $\times 20$ .)

to a point posteriorly. In *Astraspis desiderata* from the Harding Sandstone there is little or no indication of a similar variation in the shape of the tubercles from one part of the carapace to another (Ørvig, in MS., b).

The plates and scales of the exoskeleton are all remarkably stout, with their average thickness being, as in *Astraspis* and *Eriptychius*, probably greater in relation to the size of the animals as a whole than in any of the geologically younger members of the Heterostraci. They are built up of three layers—a superficial tubercle-layer; a middle, vascular layer; and a basal layer. In their general proportions these layers correspond closely to the similar layers in the exoskeleton of *Astraspis* (Bryant, 1936, pp. 418–421, pl. 2, fig. 3).

The tubercles are made up of two, sharply defined, histological constituents: (a) a thick upper layer of compact, semitransparent, sometimes faintly bluish white substance (*ezul*, *bzul*, fig. 3) which, as I shall have the opportunity of showing in another connection (Ørvig, in

MS., a), is not enamel, nor in any way enamel-like, but clearly a special variety of dentinous tissue (mesodentine); and (b) a lower part of typical aspidin which forms thick walls around a basal, "pulp" cavity (*b.as*, *pca*, fig. 3). In the tubercles of early stages of growth, the upper layer is, just as in *Astraspis* (Ørvig, in MS., a), devoid of real dentinal tubes similar to those in dentine proper (e. g., in the tubercles and ridges of the exoskeleton in *Eriptychius* and post-Ordovician Heterostraci in general), but it is, however, pierced throughout its height by numerous very fine canals which correspond, in a broad sense, to delicate ramifications of such tubes. In the tubercles of consecutive stages of growth, on the other hand, this layer is to some extent suggestive of the dentinous tissues in the exoskeleton of various early Osteostraci (Ørvig, in MS., a) in that it consists of a thick outer part with the same fine canals as those just referred to (*ezul*, fig. 3), and, in addition, of a thin, inner part containing a system of short, stemlike dentinal tubes or, in some cases, elongated cell-spaces, from which these fine canals issue in a superficial direction (*bzul*, *dt''*, fig. 3). A similar inner part of the dentinous tissue, exhibiting dentinal tubes or cell-spaces, is absent altogether in all tubercles of the exoskeleton in *Astraspis*.

The aspidin in the lower part of the tubercles is perfectly similar histologically to that in the middle and basal layers of the plates and scales. As in *Astraspis*, it is penetrated by fine fibers of Sharpey radiating from the "pulp" cavity (Bryant, 1936, p. 419, pl. 3; pl. 4, fig. 2; pl. 7, fig. 2; Gross, 1954, p. 80, pl. 3, fig. 2; pl. 5, figs. 3, 4). In the tubercles of early stages of growth this cavity is always undivided and completely separated from the upper dentinous tissue by the thick layer of aspidin which forms its roof (see Gross, 1954, pl. 5, figs. 3, 4). In the tubercles of subsequent stages of growth, however, a system of fairly thin, straight vascular canals issue in a radiating manner from the upper part of the "pulp" cavity, terminating close beneath and sometimes almost at the boundary between the aspidin and the outer dentinous tissue (*can.pca*, fig. 3). This system of vascular canals has no connection whatever with the short dentinal tubes or cell-spaces in the inner part of the dentinous tissue. A similar canal system is not developed in the tubercles in *Astraspis*, but may possibly have existed in the predecessors of that form (Ørvig, in MS., a).

The nature of the hard tissues of the tubercles will be dealt with elsewhere (Ørvig, in MS., a) and will not be commented upon further here. Of interest to us in the present connection is above all the fact that, by their microstructure, the tubercles of early stages of growth invariably are sharply distinguishable from those of subsequent stages of growth (clearly shown, e. g., by sections prepared of

specimens exhibiting simultaneously both the immature and mature types of ornamentation). This is surprising in view of the condition of the exoskeleton in a great many other lower vertebrates where the dentine tubercles belonging to consecutive generations certainly may show varying degrees of complexity and hence may differ to some extent from each other (see, e. g., Ørvig, 1957, p. 388), but nevertheless are always basically similar in their histological structure.

The middle, vascular layer is thick, and its vascular canals are irregularly distributed except in some of the polygonal plates of the carapace where they may, occasionally, show a more or less distinct "transsutural" arrangement near the marginal faces (see Delpy, 1942, pp. 52-53; Ørvig, in MS., a). Ontogenetically this layer arose as a system of thin, bony trabeculae separated by fairly wide vascular spaces, but later on it became rather compact (more so, in fact, than the corresponding layer of the exoskeleton in most post-Ordovician Heterostraci) by the deposition of thick-walled primary osteons on the margins of the trabeculae. The osteons, which are perfectly similar to those in *Astraspis* (Bryant, 1936, pl. 6, pl. 7, fig. 1; Ørvig, 1951, pl. 3, figs. 3, 4) and to those in various Psammosteids as well (Gross, 1954, pl. 5, fig. 11), are penetrated by fine fibers of Sharpey radiating from the vascular canals.

The basal layer was somewhat thin in early ontogenetic stages, but subsequently it increased considerably in thickness by the apposition of new aspidin lamellae on its inner side. As far as one can judge, it is not continuous basally with layers of perichondral bone. As in *Astraspis* and *Eriptychius* (fig. 5, *b*; see Bryant, 1936, pp. 421, 425, pl. 2, fig. 3; pl. 13, fig. 1), but contrary to the case in all Silurian and Devonian Heterostraci, it is penetrated throughout its extent by a great many vascular canals, ascending with about equal interspaces from the subcutaneous (subaponeurotic) vascular plexus beneath the exoskeleton. The presence of this system of ascending vascular canals, whose more or less funnel-like openings are spread all over the basal face of the plates and scales (pl. 1, fig. 5; Bryant, 1936, pl. 5, fig. 2), is no doubt a primitive condition (Ørvig, in MS., a).

It is worthy of mention that the *Pycnaspis* plates from the Winnipeg formation of the Williston Basin in Montana and the Whitewood formation in South Dakota referred to above (p. 8) exhibit stout, mushroom-like tubercles which in shape and microstructure are similar to those belonging to mature stages of growth in *Pycnaspis splendens*, new genus, new species (pl. 2, figs. 1-3). These plates are undoubtedly referable to *Pycnaspis*, new genus, but for the time being, at least, they cannot be determined as to species.

### Other vertebrates

The great majority (at least 75 percent) of the plates and scales in the material from the Rock Creek locality at my disposal belongs to *Pycnaspis splendens*, new genus, new species, but there are also several (about 20 percent) referable to the Eriptychiida, probably to a new genus of this group, and some few to *Astraspis*? sp. In addition, the fauna may also include exoskeletal elements of other forms whose systematic position is at present indeterminable. On the other hand, the *Pycnaspis*-bearing beds do not seem to contain pieces of bone tissue with cell-spaces or pieces of globular calcified cartilage, like those met with in the Harding Sandstone of Colorado (Ørvig, 1951, p. 381, fig. 18A) and the Winnipeg formation of the Williston Basin in Montana. To what extent those beds are devoid of other microfossils, such as lingulid shells, conodonts, etc., cannot be decided with any certainty on the basis of the limited material dealt with here.

The plates belonging to *Astraspis*? sp. (fig. 4) are of approximately the same order of size as those of *Pycnaspis splendens*, new genus, new species, with the mature type of ornamentation, but clearly distinguishable from the latter by the shape and microstructure of their tubercles (fig. 2, *b*, pl. 1, figs. 1-4; cf. also pl. 2, figs. 1-3). These tubercles, which vary considerably in size, all consist of a pointed crown with deep, radiating grooves, and a conical neck-portion, which is frequently comparatively high. In their microstructure, they are similar to those in *Astrapis desiderata* (Bryant, 1936, pp. 418-420, pl. 2, fig. 3; pls. 3, 4; pl. 5, figs. 1, 3; Ørvig, 1951, fig. 22B; in MS., a; Gross, 1954, pl. 3, fig. 2; pl. 5, figs. 3, 4) and those belonging to early stages of growth in *Pycnaspis splendens*, new genus, new species.

Most of the material of Eriptychiida gen. and sp. indet. comprises fragments of plates, frequently of large size, whose ornamentation consists of fairly low and broad tubercles. These tubercles (fig. 5, *a*)—which as a rule are considerably coarser than those of the *Eriptychius* plates from the Harding Sandstone of Colorado (Walcott, 1892, pl. 4, figs. 8, 9; Bryant, 1936, pl. 8, fig. 1) and the Winnipeg formation of the Williston Basin in Montana (Ørvig, in MS., a)—are fairly low, elongated pearshaped or irregular in outline, and smooth on top; they have no well-defined neckportion and they are frequently arranged in more or less distinct rows (pl. 2, figs. 4, 5, 7). As in *Eriptychius* (fig. 5, *b, c*; Bryant, 1936, pl. 11) and in the post-Ordovician Heterostraci in general, these tubercles consist entirely of ordinary dentine. In their basal part, there is no large pulp cavity but a system of vascular canals from which the dentinal tubes issue in a superficial direction (for further details concerning the microstructure, see Ørvig, in MS., a). In only one of the plates is the position in the cuirass of the living



animal determinable with any degree of certainty. This specimen, which is particularly large and well preserved, in all probability represents a branchio-cornual plate, unknown so far in any of the pre-Silurian Heterostraci (pl. 2, figs. 4-7). A second specimen, which may

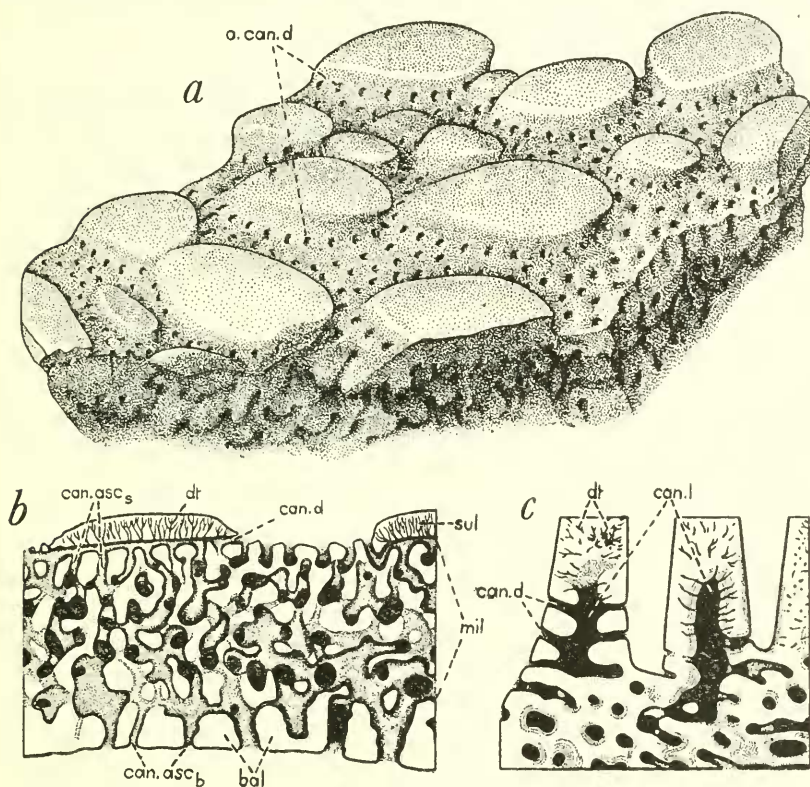


FIGURE 5.—*a*, *Eriptychiida* gen. and sp. indet.: Ornamentation of a plate-fragment from the *Pycnaspis*-bearing beds of the Rock Creek section, in oblique lateral view (mainly after USNM 21339,  $\times 36$ ). *b*, *c*, *Eriptychius* sp., Winnipeg formation, Williston Basin, Mont., sections of scales (from Ørvig, in MS, *a*): *b*, Vertical section showing the dentine ridges of the external face (cut somewhat obliquely to their axes of length), the middle, vascular layer, and the basal layer (section No. S 1438;  $\times 36$ ); *c*, horizontal section of the dentine ridges and the adjoining part of the middle, vascular layer (section No. S 1454;  $\times 36$ ). Explanation of symbols: *bal*, basal layer of the scales; *can.asc.b*, ascending vascular canals piercing the basal layer; *can.asc.s*, vascular canals in the upper part of the middle layer of the scales, ascending towards the dentine ridges; *can.d*, short vascular canals extending outwards in the basal part of the dentine ridges and opening to the exterior at the basal circumference of those ridges; *can.l*, longitudinal vascular canals in the basal part of the dentine ridges; *dr*, dentinal tubes; *mil*, middle, vascular layer of the scales; *o.can.d*, the openings of vascular canals at the basal circumference of the dentine ridges; *sul*, superficial layers of the scales.

well be the broken-off anterior part of another branchio-cornual plate, shows a wide canal in its interior that may, perhaps, be a lateral line canal (*llc?*, pl. 2, fig. 8). If this interpretation is correct, there may be some reason to believe that in the Eriptychiida the lateral line system had no such superficial position as in *Astraspis* (Ørvig, in MS., b), but that, like in several younger Heterostraci, it lay partly, or entirely, in the middle, vascular layer of the exoskeleton.

Apart from the plates dealt with here, the material of Eriptychiida gen. and sp. indet. from the *Pycnaspis*-bearing beds also includes a certain amount of scales of much the same kind as those of *Eriptychius americanus* from the Harding Sandstone of Colorado (Walcott, 1892, pl. 4, figs. 5, 6, 11; Bryant, 1936, pp. 423-424, pl. 8, fig. 2; pl. 9, fig. 2) and *Eriptychius* spp. from the Winnipeg formation of the Williston Basin in Montana and the Whitewood formation of South Dakota. These scales, which vary somewhat in size, consist of an anterior overlapped portion without ornamentation and a posterior exposed portion exhibiting a system of roughly parallel dentine ridges. As in the scales of *Eriptychius* from the Harding Sandstone and other formations, the dentine ridges are highly reminiscent of those of the exoskeleton in the Cyathaspida and Pteraspida (see Lindström, 1895, fig. 2; Kiær and Heintz, 1935, pl. 37; Gross, 1935, fig. 5c; and others) in that they contain, in their basal part, a longitudinal vascular canal from which a series of short vascular canals issue with fairly regular interspaces to both sides (*can.l*, *can.d*, fig. 5, b, c; concerning this canal system see also Ørvig in MS., a). In the material from the *Pycnaspis*-bearing beds there are also a few scales of large size ornamented with fairly coarse tubercles (pl. 3, figs. 5, 6) that are to some extent suggestive of the median dorsal and median ventral ridge-scales of the trunk in several post-Ordovician Heterostraci, e. g. the Cyathaspida, Pteraspida, and Psammos-teida (see Kiær and Heintz, 1935, figs. 41-44, *md* and *mv* of fig. 50; White, 1935, figs. 1, 2, 63, 65; Obrutchev, 1945, figs. 2-5; and others). As far as one can tell at present, scales of this particular kind are not met with in the *Eriptychius* material from the Harding Sandstone of Colorado and the Winnipeg formation of the Williston Basin in Montana.

### Discussion

There is surely reason to believe that, as they become better known, the Ordovician vertebrates of North America will prove highly useful for correlation purposes, but up to now there has been very little information in the literature as regards their stratigraphical distribution. It may be of some interest in this respect that, according to

what has been said in this paper, one may now distinguish two different vertebrate faunas in the Ordovician of the Cordilleran Region, one in the Harding Sandstone of Colorado and another in the *Pycnaspis*-bearing beds of the Bighorn Mountains of Wyoming. In addition, there is probably also a third vertebrate fauna—intermediary, to some extent at least, between the other two—in the material at my disposal from the Winnipeg formation of the Williston Basin in Montana. The latter material has not yet been investigated in detail, but a preliminary examination has shown that it includes plates and scales of *Eriptychius* sp. (possibly a new species), *Astraspis* sp., *Pycnaspis* sp. indet. (see p. 8 and pl. 2, figs. 1–3) and surely also of other forms at present indeterminable as to genus. A particularly interesting specimen from this material is a large, keel-like plate, ornamented on its external face with a system of broad, inosculating dentine ridges (pl. 3, figs. 1–4); it may, perhaps, belong to a new representative of the Eriptychiida.

### Bibliography

- AMSDEN, T. W., and MILLER, A. K.  
 1942. Ordovician conodonts from the Bighorn Mountains of Wyoming. Journ. Paleont., vol. 16, No. 3, pp. 301–306, 2 figs., 1 pl.
- BAIRD, DONALD  
 1955. Latex micro-molding and latex-plaster molding mixture. Science, new ser., vol. 122, p. 202.
- BEHRE, C. H., and JOHNSON, J. H.  
 1933. Ordovician and Devonian fish horizons in Colorado. Amer. Journ. Sci., ser. 5, vol. 25 (225), pp. 477–486.
- BERG, L. S.  
 1940. Classification of fishes, both recent and fossil. Trudy, Zool. Inst. Acad. Sci. U. R. S. S., vol. 5, No. 2, pp. 85–517, 190 figs. (Russian and English.)  
 1955. Classification of fishes and fish-like animals, living and fossil. Ed. 2. Trudy, Zool. Inst. Acad. Sci. U. R. S. S., vol. 20, 286 pp., 263 figs. (In Russian.)
- BRANSON, E. B., and MEHL, M. G.  
 1933. Conodont studies, No. 1: Conodonts from Harding Sandstone of Colorado . . . . Missouri Univ. Studies, vol. 8, No. 1, pp. 1–72, 1 fig., 4 pls.
- BRYANT, W. L.  
 1927. Evidence of the presence of chordates in the Cambrian. 15th Ann. Rep., Vermont State Geologist, 1925–26, pp. 125–126, 1 fig.  
 1936. A study of the oldest known vertebrates, *Astraspis* and *Eriptychius*. Proc. Amer. Phil. Soc., vol. 76, No. 4, pp. 409–427, 13 pls.
- BYSTROW, A. P.  
 1955. The microstructure of the shield of *Agnatha*, the jawless vertebrates from Silurian and Devonian periods. Berg. Mem. Vol., Moscow, Acad. Sci. U. R. S. S., 1955, pp. 472–523, 46 figs. (In Russian.)

## BYSTROW, A. P.

1956. On the damage caused by fungi in the skeletal elements of fossil animals. *Leningrad Universitet Vestnik*, vol. 11, No. 6, *Serica Geologo-Geografich*, No. 1, pp. 30-46, 13 figs. (In Russian.)

## COCKERELL, T. D. A.

1913. Ordovician (?) fish remains in Colorado. *Amer. Nat.*, vol. 47, No. 556, pp. 246-247.

## CULLISON, J. S.

1938. Dutchtown fauna of southeastern Missouri. *Journ. Paleont.*, vol. 12, No. 3, pp. 219-228, pl. 29.

## DARTON, N. H.

- 1906a. Geology of the Bighorn Mountains. *U. S. Geol. Surv. Prof. Papers*, No. 51, 129 pp., 14 figs., pls. 1-47.  
1906b. Fish remains in Ordovician rocks in Bighorn Mountains, Wyoming, with a résumé of Ordovician geology of the Northwest. *Bull. Geol. Soc. Amer.*, vol. 17, pp. 541-566, 6 figs., pls. 73-79.  
1909. Discovery of fish remains in Ordovician of the Black Hills, South Dakota. (Abstract.) *Bull. Geol. Soc. Amer.*, vol. 19, pp. 567-568.

## DEAN, BASHFORD

1906. Chimaeroid fishes and their development. *Carnegie Inst. Washington*, Publ. No. 32, pp. 1-194, 144 figs., 11 pls.

## DELPEY, GENEVIÈVE (MME. TERMIER)

1942. Un cartilage calcifié fossile. *Bull. Soc. Geol. France*, ser. 5, vol. 12, pp. 45-56, 8 figs., 1 pl.

## DENISON, R. N.

1956. A review of the habitat of the earliest vertebrates. *Fieldiana, Geology*, vol. 11, No. 8, pp. 359-457.

## EASTMAN, C. R.

1907. Devonian fishes of the New York formations. *Mem. New York State Mus.*, No. 10, pp. 1-235, 34 figs., 15 pls.  
1917. Fossil fishes in the collection of the U. S. National Museum. *Proc. U. S. Nat. Mus.*, vol. 52, No. 2177, pp. 235-304, 9 figs., 23 pls.

## EHLERS, ALLEN

1943. Williston Basin wildcat tests, Oliver County, North Dakota. *Bull. Amer. Assoc. Petr. Geol.*, vol. 27, No. 12, pp. 1618-1622.

## FLOWER, R. H.

1952. Cephalopods from the Harding and Manitou formations of Colorado. *Journ. Paleont.*, vol. 26, No. 3, pp. 505-518, 2 pls.

## FREDERICKSON, E. A., AND POLLACK, J. M.

1952. Two trilobite genera from the Harding formation (Ordovician) of Colorado. *Journ. Paleont.*, vol. 26, No. 4, pp. 641-644, 6 figs.

## FURNISH, W. M.; BARRAGY, E. J.; AND MILLER, A. K.

1936. Ordovician fossils from upper part of type section of Deadwood formation, South Dakota. *Bull. Amer. Assoc. Petr. Geol.*, vol. 20, No. 10, pp. 1329-1341, 1 fig., 2 pls.

## GILL, E. D.; CASTER, K. E.; AND BOSWELL, P. C. R.

1956. Simple apparatus for vacuum injection of moulding latex. *Australian Journ. Sci.*, vol. 18, No. 6, pp. 198-199.

## GREGORY, W. K.

1951. Evolution emerging. A survey of changing patterns from primeval life to man. Vol. 1, 762 pp.; vol. 2, 1013 pp., illus.



## GROSS, WALTER

1935. Histologische Studien am Aussenskelett fossiler Agnathen und Fische. *Palaeontographica*, vol. 83, Abt. A, 60 pp., 30 figs., 7 pls.
1950. Die paläontologische und stratigraphische Bedeutung der Wirbeltierfaunen des Old Reds und der marinen altpaläozoischen Schichten. *Abh. Deutsch. Akad. Wiss., Math.-Naturw. Kl. Jahrg. 1949*, No. 1, 130 pp., 1 fig.
1954. Zur Conodonten-Frage. *Senckenbergiana Lethaea*, vol. 35, pp. 73-85, 2 figs., 5 pls.

## HOWELL, B. F.

1937. Cambrian *Centropleura vermontensis* fauna of northwestern Vermont. *Bull. Geol. Soc. Amer.*, vol. 48, No. 8, pp. 1147-1210, 6 pls.

## JAMES, W. WARWICK

1957. A further study of dentine. *Trans. Zool. Soc. London*, vol. 29, pt. 1, 66 pp., 4 figs., 10 pls.

## JOHNSON, J. N.

1944. Paleozoic stratigraphy of the Sawatch Range, Colorado. *Bull. Geol. Soc. Amer.*, vol. 55, No. 3, pp. 303-378, 7 figs., 11 pls.

## KJÆR, JOHAN, AND HEINTZ, ANATOL

1935. The Downtonian and Devonian vertebrates of Spitsbergen. 5. Suborder *Cyathaspida*. *Skrift. Svalb. Ish.*, No. 40, 138 pp., 57 figs., 40 pls.

## KIRK, EDWIN

1930. The Harding Sandstone of Colorado. *Amer. Journ. Sci.*, ser. 5, vol. 20 (220), No. 120, pp. 456-465.

## KIRK, S. R.

1929. Conodonts associated with the Ordovician fish fauna of Colorado—a preliminary note. *Amer. Journ. Sci.*, ser. 5, vol. 18 (218), No. 108, pp. 493-496, 1 pl.

## KVAM, THORVALD

1946. Comparative study of the ontogenetic and phylogenetic development of dental enamel. *Norsk Tannlægeforenings Tidende*, vol. 56, suppl., 198 pp., 147 figs.

## LINDSTRÖM, GUSTAF

1895. On remains of a *Cyathaspis* from the Silurian strata of Gotland. *Svensk. Vet. Akad. Handl. Bih.*, vol. 2, afd. 4, No. 3, 15 pp., 2 figs., 2 pls.

## McCABE, W. S.

1954. Williston Basin Paleozoic unconformities. *Bull. Amer. Assoc. Petr. Geol.*, vol. 38, No. 9, pp. 1997-2010, 10 figs.

## McCoy, M. R.

1952. Ordovician sediments in the Northern Black Hills. *Billings Geol. Soc., Guidebook, 3d Ann. Field Conf.*, pp. 44-47. (Not seen, cited after Denison, 1956.)

## MILLER, A. K.

1930. The age and correlation of the Bighorn formation of northwestern United States. *Amer. Journ. Sci.*, ser. 5, vol. 20 (220), No. 117, pp. 195-213.

## MILLER, A. K.; CULLISON, J. S.; AND YOUNGQUIST, WALTER

1947. Lower Ordovician fish remains from Missouri. *Amer. Journ. Sci.*, vol. 245, No. 1, pp. 31-34, 1 pl.

## OBRUTCHEV, D. V.

1945. The evolution of *Agnatha*. *Zoologicheskii Zhurnal*, vol. 24, pp. 257-272, 10 figs. (In Russian with English summary.)
1948. On the evolution of the exoskeleton in teleostomian fishes. *Bull. Acad. Sci. U. R. S. S., Biol. Ser.*, vol. 3, pp. 281-286. (In Russian.)
1956. Cephalaspids from the lower Devonian of Tova. *Comptes Rendus (Doklady) Acad. Sci. U. R. S. S.*, vol. 106, No. 5, pp. 917-919, 1 fig., 1 pl. (In Russian.)

## ÖRVIG, TOR

1951. Histologic studies of placoderms and fossil elasmobranchs. 1. The endoskeleton, with remarks on the hard tissues of lower vertebrates in general. *Svensk. Vet. Akad., Ark. Zool.*, ser. 2, vol. 2, No. 2, pp. 321-456, 22 figs., 8 pls.
1957. Remarks on the vertebrate fauna of the lower Upper Devonian of Escuminac Bay, P. Q., Canada, with special reference to the porolepiform crossopterygians. *Svensk. Vet. Akad., Ark. Zool.*, ser. 2, vol. 10, No. 6; pp. 367-426, 13 figs.
- In Studies on North American ostracoderms. 1: On certain *Osteostraci* from the lower Upper Devonian of Escuminac Bay in Canada, with remarks on the phylogeny of the dentinous tissues in lower vertebrates.
- In Studies on North American ostracoderms. 2: On *Astraspis desiderata* MS.,b Walcott.

## PEYER, BERNHARD

1945. Über Algen und Pilze in tierischen Hartsubstanzen. *Zurich, Arch. Julius Klaus-Stiftung Erg. Bd.*, vol. 20, pp. 496-546, 48 figs.

## RHODES, F. H. T., AND WINGARD, PAUL

1957. Chemical composition, microstructure, and affinities of the Neurodontiformes. *Journ. Paleont.*, vol. 31, No. 2, pp. 448-454, 2 figs.

## ROBERTSON, G. M.

1954. Some attempts at the phylogeny of the early vertebrates. *Proc. Iowa Acad. Sci.* (1953), vol. 60, pp. 725-737, 2 figs.

## ROBERTSON, J. D.

1957. The habitat of the early vertebrates. *Quart. Rev. Biol.*, vol. 32, No. 2, pp. 156-183.

## ROHON, J. V.

1889. Über unter-silurische Fische. *Bull. Acad. Imp. Sci., St. Petersburg*, new ser., vol. 1 (33), No. 2, pp. 269-277, 1 pl.

## ROMER, A. S.

1955. Fish origins—fresh or salt water? In *Papers in Marine Biology and Oceanography*, dedicated to Henry Bryant Bigelow . . . 1955. *Deep-Sea Research*, suppl., vol. 3, pp. 261-280.

## ROMER, A. S., AND GROVE, B. H.

1935. Environment of the early vertebrates. *Amer. Midl. Nat.*, vol. 16, No. 6, pp. 805-856.

## STAUFFER, C. R.

1930. The Devonian of California. *Sci. Bull. Univ. California, Dept. Geol.*, vol. 19, No. 4, pp. 81-118, 5 pls.

STENSIÖ, E. A.

- 1927. The Downtonian and Devonian vertebrates of Spitsbergen. 1: Family *Cephalaspidae*. Skrift. Svalb. Nordish., No. 12, 402 pp., 103 figs., 112 pls.
- 1948. On the *Placodermi* of the upper Devonian of East Greenland. 2: *Antiarchi*. Subfamily *Bothriolepinae*. . . . Palaeozoologica Groenlandica, vol. 2, 622 pp., 308 figs., 75 pls.

STETSON, H. C.

- 1931. Studies on the morphology of the *Heterostraci*. Journ. Geol., vol. 39, No. 2, pp. 141-154, 7 figs.

SWEET, W. C.

- 1954. Harding and Fremont formations, Colorado. Bull. Amer. Assoc. Petr. Geol., vol. 38, pp. 284-305, 4 figs.
- 1955. Conodonts from the Harding formation (middle Ordovician) of Colorado. Journ. Paleont., vol. 29, No. 2, pp. 226-262, 17 figs., 3 pls.

TIEJE, A. J.

- 1924. New earliest known vertebrates. (Abstract.) Bull. Geol. Soc. Amer., vol. 35, No. 1, p. 1620.

TWENHOFEL, W. H., ET AL.

- 1954. Correlation of the Ordovician formations of North America, by the Ordovician Subcommittee of the Committee on Stratigraphy of the National Research Council. Bull. Geol. Soc. Amer., vol. 65, No. 3, pp. 247-298, 2 figs., 1 pl.

ULRICH, E. O.

- 1938. Age of the Harding Sandstone fish remains. (Abstract.) Proc. Geol. Soc. Amer. (1937), pp 289-290.

VAILLANT, LÉON

- 1902. Sur la présence du tissu osseux chez certains poissons des terrains palaeozoïques de Canyon City (Colorado). Comptes Rendus Acad. Sci. Paris, vol. 134, No. 22, pp. 1321-1322.

WALCOTT, C. D.

- 1892. Notes on the discovery of a vertebrate fauna in Silurian (Ordovician) strata. Bull. Geol. Soc. Amer., vol. 3, pp. 153-172, pls. 3-5.

WHITE, E. I.

- 1935. The Ostracoderm *Pteraspis* Kner and the relationships of the agnathous vertebrates. Phil. Trans. Roy. Soc. London, ser. B, vol. 225, No. 527, pp. 381-457, 97 figs., pls. 25-27.

WILLS, L. J.

- 1935. Rare and new ostracoderm fishes from the Downtonian of Shropshire. Trans. Roy. Soc. Edinburgh, vol. 58, pt. 2, No. 18, pp. 427-447, 4 figs., 7 pls.

WOODWARD, A. S.

- 1921. Visit to the gallery of fossil fishes, British Museum (Natural History). Proc. Geol. Assoc., London, vol. 32, pt. 3, pp. 179-181, 2 figs.